

Lizard responses to wildfire in arid interior Australia: Long-term experimental data and commonalities with other studies

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Abstract Life in terrestrial Australian ecosystems has evolved over the past 10 million years to thrive in habitats kept in a dynamic state through fire succession cycles. Previous studies support the notion that wildfires promote species diversity in plant and animal communities by creating a heterogeneous mix of habitats, each habitat more suitable for particular subsets of species. We document population and community responses to fire in a species-rich lizard assemblage in the Great Victoria Desert of Western Australia. Lizards were censused by pit trapping at a long-unburned flat spinifex site in the Great Victoria Desert in Austral springs of 1992 and 1995. A controlled burn was undertaken in mid-October of 1995, and lizards were censused thereafter in late 1995 and early 1996, and then again in the Austral springs of 1998, 2003 and 2008. Forty-six species of lizards (2872 individuals) were collected and their stomach contents analysed over the course of a 16-year fire succession cycle at this single study site. Most strikingly, relative abundances of two species of agamids varied inversely, responding oppositely to habitat clearing effects of fire. The military dragon *Ctenophorus isolepis* reached higher abundances when vegetation was dense, and decreased in abundance in open vegetation following fire. The netted dragon *Ctenophorus nuchalis* was rare when vegetation coverage was high but increased rapidly after fire. Abundances of five species of *Ctenotus* skinks, *C. ariadnae*, *C. calurus*, *C. hanloni*, *C. pantherinus* and *C. piankai*, tracked those of *C. isolepis*. Abundance of a termite-specialized nocturnal gecko, *Rhynchoedura ornata*, increased in abundance following fire. Lizard diets changed during the course of the fire succession cycle, returning to near pre-burn conditions after 16 years. In addition to short-term fire succession cycles that contribute to structuring local communities, changes in long-term rainfall also impact desert food webs and regional biotas.

Key words: biodiversity, fire succession cycle, Great Victoria Desert, lizard, population fluctuation, secondary succession, Western Australia, wildfire.

INTRODUCTION

Wildfires, caused naturally by lightning strikes, occur frequently in most regions of the Australian continent. In sparsely populated regions of the arid interior, wildfires are permitted to burn themselves out. Burned vegetation scars the landscape, leaving mosaics of heterogeneous habitats. Such patchy vegetation heterogeneity caused by frequent burning has been proposed to be a key factor in explaining the origins and maintenance of species diversity in arid Australia (Pianka 1989; Short & Turner 1994). More generally, secondary succession following periodic environmental disturbances (fire, flooding, etc.) has been theorized to be vital to maintenance of community diversity (Horn 1974) and stability (Connell & Slatyer 1977).

Australian flora and fauna have evolved to cope with an ever-changing environment. Dominant plants in

the sandy interior deserts of Australia are perennial hummock grasses, *Triodia* and *Plechtrachne*, commonly called 'spinifex'. These hummock grasses, a unique Australian plant life form, are exceedingly flammable. Spinifex tussocks are perfectly designed for combustion, consisting of hemispherical clumps of numerous match-stick sized blades of dry curled grass filled with flammable resins, loosely interpenetrating one another and laced with ample air spaces. Spinifex is an 'ideal pyrophyte' (Pyne 1991), nearly optimal tinder (Burrows *et al.* 1991).

Geological and paleontological records indicate relatively recent changes in Australian climate. Over 10 million years, interior Australia has become drier and vegetation has transformed from forests to desert. Palynological data suggest the Australian climate was historically dominated by rainforest type plants and that aridity increased during the late Pleistocene (Martin 1990, 1991). Additionally, counts of carbonized particles indicate an increase in fires in south-eastern Australia. Sand dune habitats in the Simpson

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Desert of Central Australia are dated to be at least one million years old based on isotopic measurements from drill cores (Fujioka *et al.* 2009).

While many fires are started by lightning, the first human residents of Australia also became part of natural fire cycles. Most early explorers and historians of Australia commented on the extent to which Aborigines exploited fire (Bowman 1998). Burning spinifex grasses give off dark smoke, which can be seen from afar. Australian Aborigines used fire to send long distance smoke signals, to manage habitats and keep terrain open, as well as to facilitate capture of various animals for food. Some think that the extensive grasslands in Australia were formed and maintained by regular Aboriginal burning and that over many thousands of years, Aborigines acted to select members of plant communities for resistance to fire or for an ability to recover quickly after a fire (Latz 1995; Bowman 1998). Frequent anthropogenic fires result in a patchwork of relatively small fire scars because new fires are extinguished when they encounter recently burned open areas. Recent reductions in Aboriginal burning practices during the mid-twentieth century have led to larger fires and consequent homogenization of vegetation, which may contribute to decreased mammal species diversity (Short & Turner 1994). In areas currently burned by Aborigines, Yibarbuk *et al.* (2001) found greater abundance and diversity of large game animals and edible plants and an absence of exotic plants. Diversity of some living groups may be attributed to habitat heterogeneity caused by frequent wildfires.

Lizard species richness is higher in arid Australia than anywhere else in the world (Pianka 1969, 1996). Milewski (1981) suggested that infertile soils of central Australia contribute indirectly to promote high reptile diversity. Morton and James (1988) expanded Milewski's argument, proposing that the combination of low erratic rainfall and nutrient poor soils promote spinifex grasses, which support few herbivores except for termites, which in turn sustain the high numbers of species of Australian desert lizards. In another analysis of lizard species richness, James and Shine (2000) showed that geographic ranges of arid zone skink species are larger than those from other areas and suggested that the sheer size of the Australian arid zone was pivotal to understanding lizard diversity; however, both papers overlooked the importance of fire in promoting habitat heterogeneity. More recently, Orians and Milewski (2007) proposed an elaborate 'Nutrient-Poverty/Intense-Fire Theory' suggesting that numerous features of organisms and ecosystems of Australia, including its high lizard diversity, are evolutionary consequences of adaptations to nutrient shortages, compounded by intense fires that tend to occur as a result of nutrient poverty. They also neglected the importance of spatial-temporal habitat

heterogeneity caused by fires in promoting high numbers of species.

Vertebrate animal response to wildfire has a larger literature for Australia than for any other continent. Lizards, in particular, have been studied at 20 sites in all regions of continental Australia plus New Zealand (see Appendix S1 for a summary of past studies with information on locality, study type and sample sizes). Many studies include data on whole communities where abundance data for an entire lizard assemblage was recorded. Others focus on population response within a single species. Griffiths' (1995) population study of frilled necked lizards is the only published study where individuals were tracked using radiotelemetry during a fire, providing the only information on what individuals are doing during and immediately following a wildfire.

A few studies on reptile responses to controlled fires conducted in North America deserve mention. These studies encompass very different kinds of fire prone habitats, including an iguanid lizard (Lee 1974), a skink (Mushinsky 1985; Mushinsky & Gibson 1991) and a herpetological assemblage (Litt *et al.* 2001) in the sandhills of Florida, an iguanid lizard (Lillywhite & North 1974; Lillywhite 1977), a whole squamate assemblage (Simovich 1979) in chaparral scrub forests of southern California and a squamate assemblage in a Kansas prairie (Wilgers & Horne 2006). In all of these studies, moderate and periodic burning was associated with higher species richness or increased population sizes.

Past fire studies can be distinguished by data-collecting methods. All but three studies listed in Appendix S1 use the chronosequence method, which means data are examined comparatively from areas known to have burned at different times. This allows many years worth of data to be collected over a shorter time. While useful, this method has clear limitations because of confounding factors involving site-specific differences among study plots. Differences between recently burned and long since burned plots may have different biological properties for many reasons, including soil chemistry, topology or even proximity to other sites with very different physical or biological properties. An ideal protocol for studying community responses to wildfire would use replicated experiments by tracking population abundances over time before and after controlled fires. Experimental sites would need to be far apart to eliminate pseudoreplication and population fluctuations that result from immigrants fleeing from other recently burned areas. Sampling across many different sites while simultaneously sampling over many years is not feasible for most studies. We approach ecological responses to wildfire by using long-term ecological data from a single large study site. Our study could not be replicated because of limited

available manpower; however, we did sample another unburned study site with more complex vegetation 4 km north simultaneously which can be viewed as a limited control.

Habitat change as a result of wildfire may alter arthropod populations, which in turn affect populations of their predators such as lizards. Much variation exists within and between major taxonomic groups in arthropod responses to fire. Spiders in Western Australia decrease in abundance following fire (Langlands *et al.* 2006), stick insects generally decrease in abundance if their eggs are burned (Bedford 1979), and species within Hemiptera exhibit various responses whether in Missouri (Cancelado and Yonke 1970) or England (Morris 1975). Ants in Victoria, Australia, exhibit increased surface activity following fire, but less is known about actual change in abundance (Andersen and Yen 1985). Grasshoppers in Kansas, USA, have higher species evenness but lower total abundance in infrequently burned plots (Evans 1984, 1987). Termites are a vital prey source to some dietary specialist lizards at our study site, so changes in termite abundance following fire may result in respective changes in their predators. Previous studies on termite responses to wildfire show conflicting results. Termites of four genera in Ghana, Africa, have more colonies in fire-protected areas (Benzie 1986), whereas termites of two different genera in Zambia, Africa, have colonies at a higher density on recently burned plots (Trapnell *et al.* 1976).

Here we present data from a long-term ecological experiment, which sought to document population and community responses to fire in a species-rich lizard assemblage. Collections cover a 16-year time span and comprise two fire succession cycles. The experiment was conducted in the Great Victoria Desert of Western Australia on a spinifex (*Triodia*) grass-covered sandplain. The lizard assemblage at this site shares species with assemblages studied by Caughley (1985), Dell and How (1995), How (2002), How and Dell (2004), Letnic *et al.* (2004), Longmore and Lee (1981), Masters (1996), Mather (1979), Trainor and Woinarski (1994), and Driscoll and Henderson (2008). For most species, differences in numbers of individuals captured in mature vegetation plots *versus* recently burned habitats are either negligible or samples are too small to detect significant differences. However, three species recorded from multiple studies stand out in showing major differences in estimated population sizes between old burn and recently burned plots. *Ctenophorus nuchalis* and *Rhynchoedura ornata* were more abundant on recently burned areas (Masters 1996; How & Dell 2004). *Ctenophorus isolepis* were less abundant in recently burned habitat relative to mature vegetation (Masters 1996; Dickman *et al.* 1999; How & Dell 2004). Daly *et al.* (2007, 2008) concluded that alternating population cycles of *C. isol-*

epis and *C. nuchalis* result from differences in habitat preference. Relatively higher abundance of *R. ornata*, a termite-specialized nocturnal gecko, at recently burned plots has been observed but not explained (Caughley 1985; Masters 1996).

METHODS

Field collection

In 1992, Eric R. Pianka established the B-area ('Burn') on a long unburned, nearly pure spinifex (*Triodia basedowi*) grass-covered sandplain in the Great Victoria Desert of Western Australia 140 km east of Laverton at latitude 28°13'30"S, longitude 123°35'30"E. An aerial photo taken in February 1993 is shown in Figure 1. Spinifex tussocks were large, up to 1 m in diameter and 0.5 m high; vegetative coverage was extensive with only about 50% open sand. Patches of older reticulating and circular spinifex tussocks with less open area were embedded within this background vegetation (Fig. 1). Seventy-five 5-gallon bucket pitfall traps and associated drift fences were installed and checked twice daily in early morning and mid-afternoon. Snout-vent length, tail length, fresh body weight and an associated pit trap number were recorded for all lizards and snakes trapped. Lizards were collected under permits issued by the Department of Conservation and Land Management. All recorded specimens were euthanized and preserved with the permission of appropriate animal ethics committees, then catalogued by the Western Australian Museum, and shipped to The University of Texas for morphometric and dietary analyses. The initial 3-month census in 1992 was intended as a control to estimate species composition and abundances in a mature community for comparison with less mature recovery stages. In September and early October of 1995, lizards were collected for 6 weeks prior to an experimental burn. With the permission of the Laverton Shire Council and assistance from the Kalgoorlie Department of Conservation and Land Management, a prescribed burn was undertaken on 11 October 1995. An area of approximately 1 km² was burned, controlled by cutting a firebreak in a pentagon-type shape adjacent to an unpaved road.

Lizards were collected for 1 month immediately following the burn without drift fencing, then again for a fortnight in January 1996. Drift fencing was replaced and later follow-up censuses were conducted during the Austral spring seasons of 1998, 2003 and 2008. In 2000, a natural fire burned a portion of the study site, leaving some 15 traps in unburned maturing vegetation and 60 others in recently burned, open habitat, 3 years old in 2003. This unexpected occurrence allowed for continued tracking of part of the recovering habitat in addition to replicating a sample of the original experiment, which was rendered somewhat imperfect by this second fire. A total of 2872 individual lizards representing 46 species were collected at the B-area between 1992 and 2008 (22 031 trap days total). These collections represent seven different time intervals over two fire succession cycles from original long unburned to 13 years post-burn: (1992, interval 1) 3 years pre-burn, dense spinifex cover; (early 1995,

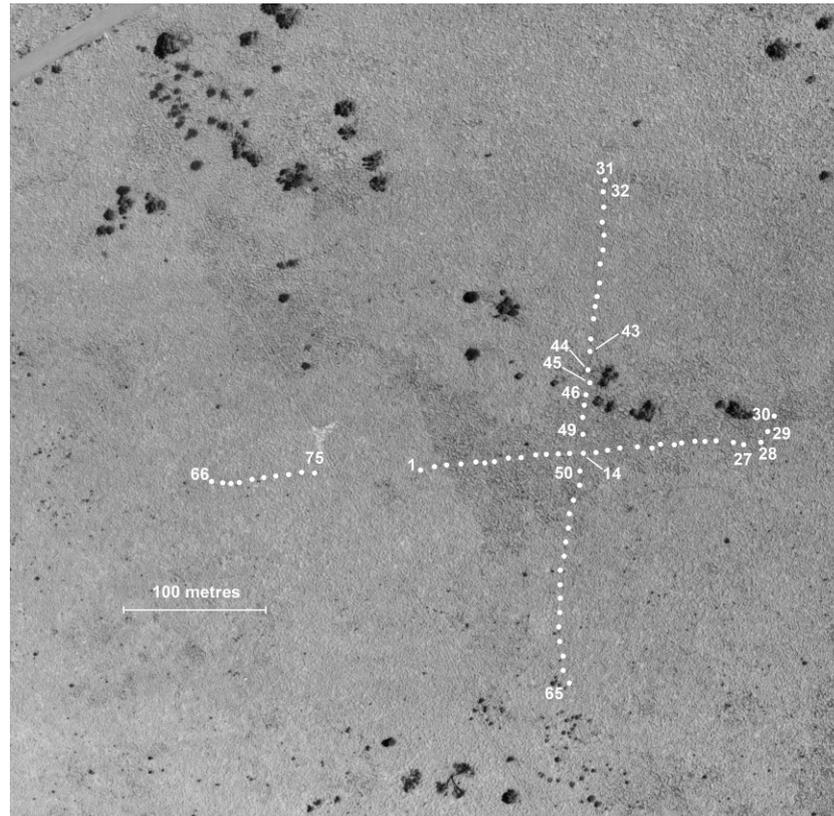


Fig. 1. Aerial photograph of the B-area taken on 17 February 1993. Positions of 75 pit traps shown with solid white circles, along with a scale. Hundreds of termitaria, circular open areas about twice the diameter of pit trap circles, are scattered about the image. Patches of older long unburned spinifex are embedded within larger patches burned more recently. Len Beadell's main east-west road from Laverton to Coober Pedy via Neale Junction is in the north-west (upper left hand) corner.

interval 2) immediate pre-burn, dense spinifex cover; (late 1995–1996, interval 3) immediate post-burn, very open with little vegetation; (1998, interval 4) 3 years post-burn, moderate vegetative cover; (2003, 60 pits, interval 5) second 3 years post-burn, small spinifex, open; (2003, 15 unburned pits, interval 6) 8 years post-burn, large spinifex; and (2008, interval 7) 13 years post-burn, moderate to dense spinifex coverage.

Laboratory analyses

Lizards were dissected, sex and reproductive state recorded, and stomachs removed. Total stomach content volume was estimated by volumetric displacement in a narrow necked graduated cylinder. Prey items within stomachs were removed and sorted into 22 prey categories, mostly arthropod orders. Items were counted and volumes estimated to the nearest cubic millimetre for each category. Volumes of individual prey items were estimated by placing a 1 mm thick layer of material over square millimetre grid paper to approximate total volume. Each lizard's counted stomach contents were kept individually and stored in separate vials with ethanol.

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Statistical analyses

Monthly total precipitation data were acquired from the Australian Bureau of Meteorology for Yamarna and Laverton, 10 km east and 130 km west of the study site, respectively. Thirty years of data are available for Yamarna from December 1967 to mid-1997 with a few missing months. Data are available for the same months from both sites for 224 months; these monthly totals were highly correlated (Pearson product moment correlation coefficient $r = 0.665$, $P < 0.0001$), allowing substitution of Laverton values as approximations for missing Yamarna data. Annual precipitation data for Laverton are continuous from 1900 to 2010 except for 12 years with missing data (1960, 1969–1978, 2003). Deviations from long-term mean annual precipitation over the course of the last century as well as 10-year moving averages over this time interval were plotted to document long-term climate change.

We used principal component analysis (PCA) on diet data and lizard abundance data at each time interval during the course of the fire succession cycle to extract the most important dimensions and to reveal apparent relationships between habitat change, prey availability and lizard relative abundances during the course of the fire succession cycle.

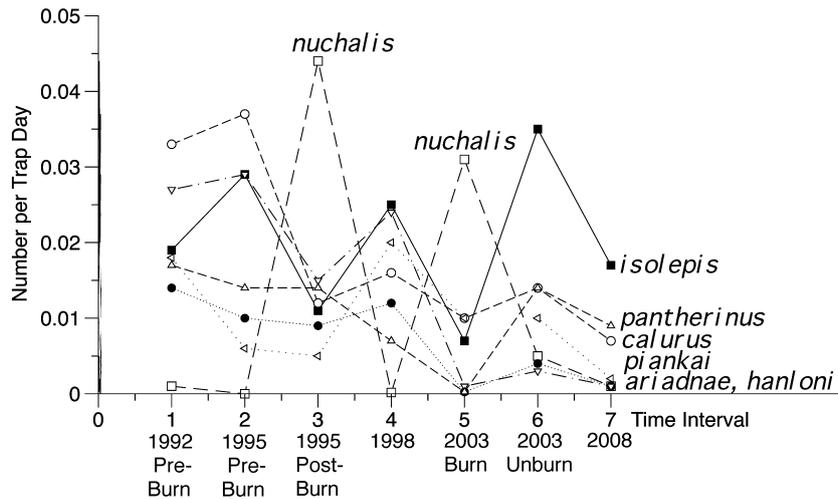


Fig. 2. Relative abundances of seven most common lizard species through 16 years. Agamids (*Ctenophorus isolepis* and *Ctenophorus nuchalis*) depicted with squares and solid and dashed lines. Skink (*Ctenotus*) species shown with various symbols and line types.

RESULTS

A few dozen scattered tussocks escaped the fire, providing limited refuges for surviving lizards. Immediately after the controlled burn, the area was walked searching for lizard fire victims but very few were found. Most lizards survived the fire by escaping into burrows. Brown hawks and crows were attracted to the burned site and sat around for days waiting for lizards to emerge. Pits were opened without drift fences for 1 month in late 1995 and again for 2 weeks in January 1996. The seven most abundant lizard species were two agamids *C. isolepis* and *C. nuchalis*, and five *Ctenotus* skinks, *C. ariadnae*, *C. calurus*, *C. hanloni*, *C. pantherinus* and *C. piankai*. Abundances varied considerably through the course of the fire succession cycle (Fig. 2). Most striking, abundances of the two agamids *C. isolepis* and *C. nuchalis* were negatively correlated, fluctuating out of phase inversely with each other, with *C. nuchalis* reaching very high population densities immediately after each burn, whereas *C. isolepis* densities diminished after fires and were more abundant in unburned or recovering vegetation cover. The netted dragon *C. nuchalis* was rare initially during pre-burn censuses in 1992 and in September – early October 1995, but increased massively in abundance immediately after the burn in late October 1995. This increase in numbers was too rapid to have been a result of reproduction, but rather appears to have been due to immigration into the area (an alternative, untestable, hypothesis is that these lizards were present before the fire but did not fall into pit traps until after the burn opened up the vegetation). Their numbers were greatly diminished just three years

later in 1998 with increased spinifex coverage. The unexpected natural wildfire burned part of the study site in 2000, clearing the vegetation, allowing *C. nuchalis* to increase again in 2003. With heavy rainfall, spinifex again recovered rapidly over the next 5 years, resulting in greatly reduced *C. nuchalis* numbers again in 2008. *Ctenophorus isolepis* became more abundant as *C. nuchalis* numbers decreased. Relative abundances of the 5 species of *Ctenotus* skinks behaved similarly to those of *C. isolepis*, with which species their abundances were positively correlated. Three species of nocturnal geckos, *Diplodactylus conspicillatus*, *D. damaeus*, and *R. ornata*, increased in abundance following fires.

Number of lizards captured per trap day was highest immediately following the controlled burn even without drift fences. Species richness and diversity peaked at 3 years post-burn in 1998. Both number of lizards captured per trap day and diversity fell afterwards (Table 1; Appendix S2). Most species were uncommon or rare.

Dietary proportions collected from all lizards of all species over the term of this 16-year study for 8 most abundant prey categories are shown in Figure 3. Orthopterans were relatively uncommon early but increased in abundance post fire, then decreased. Spiders showed the opposite trend, reaching their greatest abundance early and late in the fire succession cycle. Cockroaches were the most important food item during the 1995 pre-burn but diminished greatly thereafter. Beetles peaked in 2003 after the second fire. Termites showed two peaks, one immediately following the fire in 1995 and another in 2008, when lizard diets were again similar to those first recorded under 1992 pre-burn conditions.

Table 1. Number of species and individuals (in parentheses) in five lizard families captured at various times during the fire succession cycle, and the total number of species and total number of individuals, along with number of trap days and number of lizards captured per trap day. An expanded version is in Appendix S2

Family	1992	1995 pre-burn	1995–1996 post-burn	1998	2003 burn	2003 unburn	2008	1992–2008
Agamids	4 (93)	3 (33)	3 (113)	6 (157)	5 (169)	5 (41)	5 (73)	6 (689)
Varanids	3 (32)	1 (5)	1 (7)	3 (30)	2 (8)	3 (14)	2 (28)	3 (124)
Skinks	18 (584)	12 (95)	15 (146)	18 (608)	16 (145)	12 (60)	12 (111)	23 (1749)
Pyropodids	2 (8)	1 (2)	2 (4)	4 (34)	1 (1)	2 (5)	3 (7)	4 (61)
Geckos	6 (15)	2 (2)	5 (69)	6 (44)	8 (67)	5 (14)	6 (12)	10 (223)
Total no. species	33	19	26	37	32	27	28	46
Total individuals	731	137	339	873	400	134	231	2872
Trap days	4350	900	1850	5850	4146	1035	3900	22 031
Lizards per trap day	0.168	0.152	0.183	0.149	0.096	0.129	0.059	0.129
Diversity	8.94	8.55	9.25	10.36	7.01	9.23	6.22	12.06

Lizard species diversities calculated with Simpson's index are based on relative abundance.

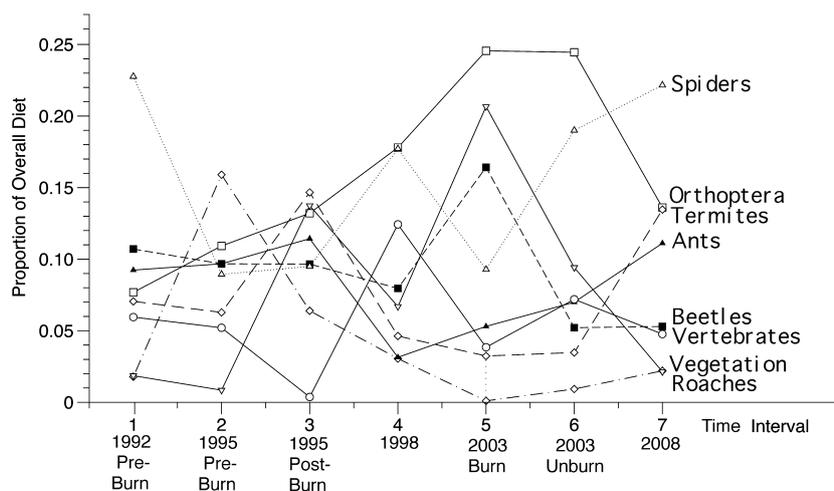


Fig. 3. Changes in relative abundances of eight most abundant food items in lizard diets through time over the course of 16 years.

Results from a PCA with sampling interval as the dependent variable, based on dietary proportions collected from all lizards of all species over the course of the 16-year fire succession cycle, for the 8 most abundant prey categories are shown in Figure 4. This plot shows the first 2 principal components of dietary niche space, depicting overall diets of all lizards for each of the 7 sampling intervals. Positions of food resources are shown with vectors emanating from 0, 0 with lengths proportional to relative importance of each prey category. Darker arrows track time intervals, showing that diets moved counterclockwise through these 2 dimensions, from 1992 to 1995 pre-burn to 95–96 post-burn to 2003 re-burn to 2003 unburned to 1998 and then to 2008 when diets returned to near 1992 pre-burn conditions.

Vegetation increased in proportional representation in lizard diets following each fire, primarily due to the

increase in abundance of *C. muchalis*, which feeds on plant material. Vertebrate prey diminished during both fires. This kaleidoscope of changing prey abundances during the course of the fire succession cycle presumably has an impact on the abundances of various lizard species, although of course, changing relative abundances of lizards also impacts the overall diet of all lizard species. Dietary information from 2872 individual lizards collected over the term of this 16-year study underscore trophic mechanisms that might explain why certain populations decline in the wake of wildfire, whereas others thrive.

A second PCA was run with abundances of the 46 different species as the dependent variable and 7 sampling intervals as the independent variable (Fig. 5). The first 2 principal components capture 91.7% of the variance. Most species clumped tightly together in the lower left of this figure, but two species, the diurnal

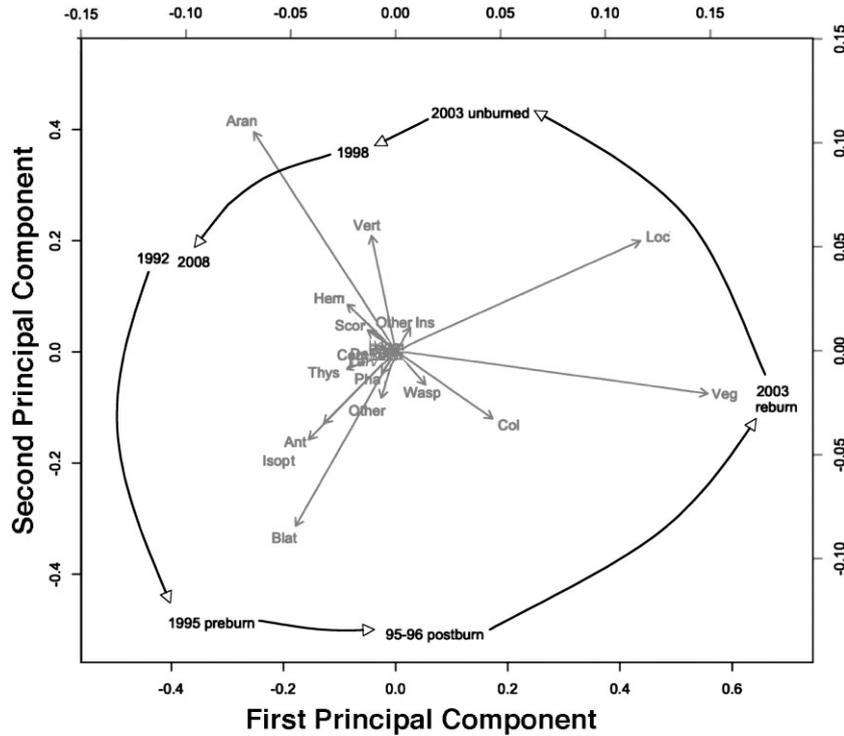


Fig. 4. Plot of first two components of dietary niche space showing overall diets in principal component space at each interval over the course of the 16-year fire succession cycle. These two principal components capture 60% of total variation in diet. Positions of food categories are shown with vectors emanating from the origin at 0,0, with their lengths proportional to relative importance. Data used to generate this graph are given in Appendix S3.

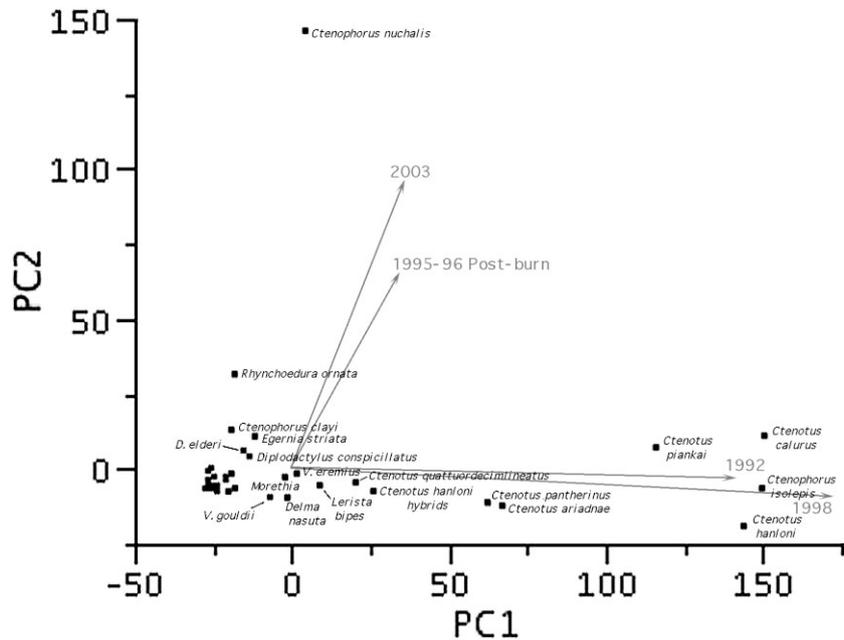


Fig. 5. Principal component analysis showing relative responses of all 46 species to fires. Two species respond positively to open habitats created by fires, and six other diurnal species respond to the denser vegetation that occurs between fires. Most species are uncommon and do not respond to fires but clump tightly together in the lower left of this figure.

agamid *C. nuchalis* and the nocturnal termite specialised gecko *R. ornata*, responded positively to open habitats created by fires (1995–1996, 2003). Six species, the agamid *C. isolepis* and five *Ctenotus* skinks *C. ariadnae*, *C. calurus*, *C. hanloni*, *C. piankai* and *C. pantherinus*, responded to dense vegetation occurring between fires in 1992 and 1998.

DISCUSSION

Termites

Morton and James (1988) proposed a megahypothesis to explain the high diversity of Australian desert lizards. They suggested that erratic unpredictable low rainfall and infertile soils promote nutrient-poor spinifex grasses, which support few herbivores. Termites, however, are able to harvest these hummock grasses, often consuming the central part of a tussock, which then grows into a ring with a hard underground termitarium at its centre. Morton and James suggested that termites are key insect prey that sustain ectotherms, especially the high numbers of Australian desert lizard species. Pianka (1989) challenged their arguments comparing diets of Kalahari desert lizards with those in Australia; termite consumption is higher in the Kalahari, yet lizard species richness is considerably lower than it is in Australia. Colli *et al.* (2006) provided data on termite and lizard species richness in the Brazilian grassland Cerrado, an independently evolved system with fewer species of lizards. Numbers of Cerrado lizard species are correlated with numbers of species of termites. However, despite higher species richness of termites in the South American Cerrado, lizard species richness is lower than it is in Australia. Termite consumption by lizards in the Brazilian Cerrado was examined by Costa *et al.* (2008), who found fewer termites than reported by Pianka (1989) for desert lizards in Australia and the Kalahari. Moreover, niche segregation in relation to termites as a food resource was not observed. The impact of termite abundance and species richness on lizard diversity and abundance remains unexplained.

Community responses and rarity

In addition to changes in vegetation, shifts in abundance of major prey resources such as arthropods may alter abundances of lizard species. Bottom-up effects through trophic levels could result in cascades of declines or increases of specifically adapted forms.

Most lizard species were rare or uncommon, but could nevertheless be important to community function. Do rare species persist in more stable com-

munities in spite of their rareness, or does the presence of rare species enhance the stability of ecosystems? One reason so many rare species exist may be that ecosystems have been ‘over-written many times after imperfect erasures’ (incomplete extinctions, Main 1982). Consequently, current ecosystems contain numerous relicts of their predecessors assembled under different conditions. Main (1982) suggested that rare species could be vital to long-term ecosystem sustainability, providing ‘insurance’ for the delivery of ecosystem functions by alternative means in the event of drastic environmental changes.

Trap success has fallen during the past decade. Some might assert that this is an artefact due to removal of lizards, but the 3- to 5-year intervals between sampling periods should be long enough for reproduction and migration back into the area. Moreover, no evidence of diminished trapping success was evident during any sampling period. Falling abundances are more likely to be real as they do correlate with lower precipitation during the last two sampling periods in 2003 and 2008, both on the B-area and at the Redsands study site 4 km north (Fig. 6).

Significant species responses

As in some previous studies (Masters 1996; How & Dell 2004; Letnic *et al.* 2004), the agamid *C. nuchalis* and the gecko *R. ornata* increase in abundance immediately following fire. *Rhynchoedura ornata* are complete termite specialists and are entirely nocturnal. However, termites are present throughout the fire succession cycle and are eaten by diurnal *Ctenotus* skinks. Increased abundances of *R. ornata* may be unrelated to prey availability. Alternatively, although we have no information about termite activity, termites could increase nocturnal activity after fire. Colonies might send scouts to search for vegetation remaining at the edge of burned habitat.

Rainfall versus fire

In desert ecosystems, water is a master limiting factor (Pianka 2000). By facilitating plant growth, rainfall increases combustible material, promoting future fires. Rainfall also increases plant coverage and reduces the proportion of open ground, favouring animal species that require closed habitat. Fires have the opposite effect, reducing vegetative cover and increasing open habitats, which favours other animal species that thrive in more open habitat. By opposing each other, these two forces create and maintain a dynamic spatial-temporal mosaic of habitat types in the Australian interior, which act together to maintain species diversity of both invertebrates and lizards (Pianka 1989).

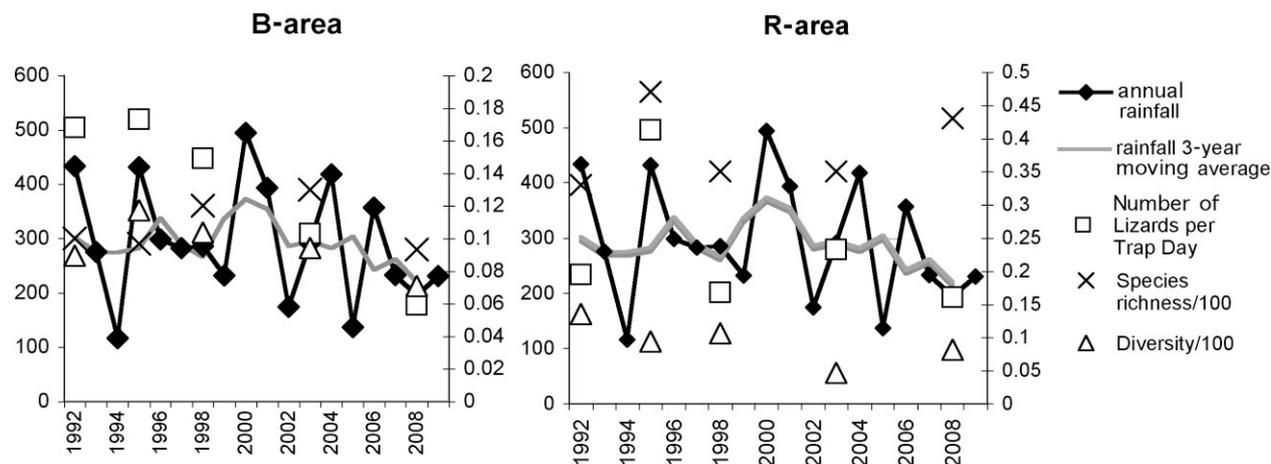


Fig. 6. Annual rainfall, 3-year moving average rainfall, number of lizards captured per trap day, species richness (number of species) and lizard diversity at various sampling intervals on the B-area and 4 km north at the R-area.

Based on the limited amount of reburn observed in satellite imagery, fire return interval in spinifex habitats over the 20-year period from 1972 to 1992 was estimated to be about 20 years (Haydon *et al.* 2000a,b). Following the 1995 controlled burn, heavy rainfall on the B-area promoted very rapid recovery of the vegetation – spinifex tussocks were large a mere 3 years later in 1998. Even more surprising, most of the B-area burned in 2000, scarcely 5 years after the 1995 burn. Spinifex roots survive fire, and regenerate above-ground leafy vegetation rapidly when sufficient moisture is available. Over the 60-month period from 1996 to 2000, an estimated 1642 mm of rainfall fell, 500 mm in excess of the long-term mean, which allowed the vegetation to recover quickly and fuel the second fire.

Global climate change has had a massive impact on Australian rainfall and will likely threaten much of the biota as well (Arnold 1988; Hughes 2003). The Australian Bureau of Meteorology has documented long-term changes in climate. Most notably, the eastern two-thirds of the continent have dried out over the last four decades whereas rainfall in most of interior Western Australia has increased by 20–50% (Australian Meteorological Bureau (2010), Link: http://reg.bom.gov.au/cgi-bin/silo/reg/cli_chg/trendmaps.cgi?variable=rain®ion=aus&season=0112&period=1970). Deviations from the long-term mean annual precipitation for Laverton are shown in Appendix S4.

Increased precipitation in the WA part of the Great Victoria Desert has increased the rate of accumulation of combustible material, which appears to have shortened the fire return interval. Recent wildfires have been very hot, large and continuous, which may reduce habitat heterogeneity and could negatively impact species richness of invertebrates and lizards. Climate change also appears to have led to shrub encroachment at the expense of spinifex hummock

grasses. Such changes in vegetation no doubt have also had an impact on food webs, community structure and regional biotas.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Summary of past studies.

Appendix S2. Complete census data for the study.

Appendix S3. Dietary data used in Figure 4.

Appendix S4. Deviations from long-term average precipitation for 110 years of rainfall data from Laverton, WA.